SELECTION FOR A DELAYED SIMULTANEOUS WING MOLT IN LOONS (GAVIIDAE)

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A simultaneous molt of the remiges, with its concomitant flightless period, is a feature widespread in the class Aves. It has been recorded for members of no less than ten orders of flying birds: Gaviiformes (Palmer, 1962), Podicipediformes (Palmer, op. cit.), Procellariiformes (Murphy, 1936), Pelecaniformes (Palmer, op. cit.), Phoenicopteriformes (Palmer, op. cit.), Anseriformes (Delacour, 1954), Gruiformes (Van Tyne and Berger, 1959: Witherby et al., 1940), Charadriiformes (Storer, 1960), Coraciiformes (Van Tyne and Berger, op. cit.), and Passeriformes (Sullivan, 1965). Knowledge of the considerable expenditure of energy required for the replacement of feathers has led to the conclusion that molt is normally a prolonged process and that rapid feather replacement develops only as a result of strong environmental selection (Humphrey and Parkes, 1959). For the remiges the consensus seems to be that simultaneous molt occurs only when it is the sole means by which a species can survive. This is perhaps true for loons as is discussed below, but two reasons suggest it may not be the case for all such birds, namely seasonal fluctuations in the abundance of food, and the extra energy required for flight by birds undergoing a gradual wing molt. It is possible that some of the wide variety of species with a simultaneous wing molt occupy niches in which either method could occur, but that rapid replacement confers slight advantages and therefore has been selected.

A simultaneous loss of the remiges is probably a necessity for loons. D. B. O. Savile (1957) states, "The Common Loon (*Gavia immer*) is a flying anachronism. . . . It has an appallingly high wing loading and a very inefficient wing form. Under these handicaps it takes off only with difficulty, after a long run, and climbs shallowly." It seems likely in a species so poorly designed for flight that the loss of even one remex from each wing would be a considerable handicap.

Typically the simultaneous loss and replacement of flight feathers is a post-breeding, late summer or early fall phenomenon—a phase of the prebasic molt. Hornbills, the coraciiform example, are exceptions, for females of certain species are flightless during breeding. The habit of the male sealing the female in the nest cavity provides the ecological opportunity. The three large species of loons are also exceptions. In adults of the Common Loon, Yellow-billed Loon (*Gavia adamsii*), and Arctic Loon (*G. arctica*) remigial replacement occurs in late winter while the birds are in their winter range.

Of the more than 40 dead Common Loons I have found along the beaches in Florida from November through June, eight were flightless, and these eight were all February birds.

Features of the life history of loons suggest some of the selective forces that may have brought about the delay of the remigial portion of the prebasic molt. The Common Loon will be used to present these ideas since more is known about its biology, primarily through the work of Olson and Marshall (1952), than is known about the other three species. Common Loons reach the breeding lakes in Canada and northern United States from mid-May to the latter half of June. After arriving at least two weeks are required to establish a territory, choose a nest site, build the nest, and lay their one or two eggs. Incubation requires another four weeks. Care of the young, which normally continues until they can fly, requires an additional 10 or 11 weeks. Thus even if a pair of Common Loons were to begin breeding at the earliest possible time, mid-May, they would be caring for young until mid-September. With actual cases it is later; Olson and Marshall (op. cit.) recorded the first flying young on 9 October in Minnesota, which is near the southern limit of the species range. Throughout this more than four-month breeding period the ability to fly is essential, for there are important aerial components in the territorial and pair-bond maintenance displays of the Common Loon.

Data are not available for the time interval between loss of the remiges and the regaining of flight in loons, but assuming it is similar to that of other water birds, ducks for example (Hochbaum, 1944), it would require three or four weeks. If loons replaced their flight feathers on the nesting lakes following breeding it would be impossible for them to leave before late October. But according to Pleva (1957) the lakes in Canada freeze over between mid-September and mid-November, and Hochbaum (op. cit.) states that ice closes the bays at Delta, in southern Manitoba, in late October or early November. Thus under present climatological conditions loons molting their remiges on the breeding lakes after nesting often would be trapped by ice and eliminated from the population. Occasionally even volant loons are trapped in this manner. Boardman (1874) reported the human slaughtering of about 30 Common Loons concentrated in a small area of open water in Big Lake, Maine. From these facts one must conclude that a simultaneous remigial molt after breeding, but before migration, is impossible.

The advantages of replacing the remiges immediately prior to spring migration probably brought about further delay once the process was postponed until after departure from the breeding areas. Movement from the nesting lakes to maritime waters is a lengthy procedure for many individuals (Palmer, op. cit.), and it is not safe for loons to become flightless on any body of water that might freeze over. Trautman (1940), for example, lists

the first week in December as the time of departure of Common Loons from Buckeye Lake in Ohio. An additional advantage is that late winter molt assures unworn feathers for the flight north and the ensuing aerial displays.

A temporary loss of the remiges while in their maritime wintering quarters is probably advantageous to loons. A reduced pectoral appendage benefits wing-propelled divers (Storer, op. cit.), and loons occasionally use this means of subsurface locomotion (Townsend, 1924). Furthermore, temporary loss of even a few buoyant feathers, and a slightly reduced cross-sectional area would be of some advantage to a foot-propelled diver.

Adult Red-throated Loons (*Gavia stellata*) and the immatures of all four species replace their remiges in summer or fall. The need for a delayed simultaneous wing molt is not as great in the Red-throated Loon for the reduced wing loading virtually eliminates the chance of their being trapped by ice. A number of observers even have seen the species take flight from land (*in* Palmer, op. cit.)! Furthermore, Red-throated Loons are decidedly more coastal than the other species, particularly during migration and in winter. According to Godfrey (*in* Palmer, op. cit.) the time of the simultaneous remigial molt in this species is from early August to November.

Immature loons of all four species replace their remiges simultaneously in summer (late May to early August in *G. immer*). But these non-breeding loons do not fly to the nesting lakes; instead they normally remain on salt water where need for wings is negligible. Thus these exceptions add strength to the hypothesis that factors associated with breeding and migration have caused the winter remigial molt in adults of the three large species of loons. Use of the morphogenetic law would suggest that the primitive condition was one of a summer wing molt, and that selection indeed has *delayed* the process in adults.

The seeming necessity for a post-migratory simultaneous wing molt in loons brings up the question of how other water birds, namely waterfowl and grebes, nesting in the same area are able to survive with a simultaneous wing molt that precedes fall migration. Data obtained at Delta, Manitoba, by Hochbaum (op. cit.) provide the answer for ducks. Males desert the females in mid summer, change into a less conspicuous eclipse plumage and replace their flight feathers well before they are needed for migration. Females continue to care for the young, but only until the first week in August when they desert the broods, no matter how immature, and replace their remiges before freeze-up. Geese undergo their wing molt while caring for the young (Kortright, 1943). Unfortunately little is known about molt in grebes although it seems certain that some forms, *Aechomophorus* for example, do shed their remiges simultaneously prior to fall migration (Palmer, op. cit.). The apparent absence of display flights (Storer, 1963) would

allow breeding and wing molt to occur simultaneously, although this is conjecture, and it may be that other factors are involved.

SUMMARY

It is suggested that adult Common Loons, and probably adults of the two other large species of *Gavia*, cannot have a gradual wing molt for structural reasons, and cannot have a simultaneous wing molt while on the breeding lakes for behavioral and climatological reasons combined. The only remaining possibility is a simultaneous molt of the remiges following fall migration. Additional selective factors have caused further delay until finally the gaining of new flight feathers immediately precedes spring migration.

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LITERATURE CITED

Boardman, C. A.
1874 A loon-atic on ice. *Forest and Stream*, 3:291.

Delacour, J.
1954 The waterfowl of the world. Vol. 1. Country Life Ltd., London.

Hochbaum, H. A.
1944 The Canvasback on a prairie marsh. The Stackpole Co., Harrisburg, Penna.

Humphrey, P. S., and K. C. Parkes
1959 An approach to the study of molts and plumages. *Auk*, 76:1–31.

Kortright, F. H.
1943 The ducks, geese and swans of North America. The Stackpole Co., Harrisburg, Penna.

Murphy, R. C.
1936 Oceanic birds of South America. Vol. 2. The Macmillan Co., New York.

Olson, S. T., and W. H. Marshall
1952 The Common Loon in Minnesota. Occas. Paper No. 5, Minnesota Mus. Nat. Hist.

Palmer, R. S.
1962 Handbook of North American birds. Vol. 1. Yale Univ. Press, New Haven and London.

Pleva, E. G., ed.
1957 The Canadian Oxford school atlas. Oxford Univ. Press, Toronto.

Savile, D. B. O.
1957 Adaptive evolution in the avian wing. *Evolution*, 11:212–224.

Storer, R. W.
1960 Evolution in the diving birds. *Proc. XIIth Internatl. Ornith. Congr.*, pp. 694–707.
1963 Courtship and mating behavior and the phylogeny of the grebes. *Proc. XIIIth Internatl. Ornith. Congr.*, pp. 562–569.

Sullivan, J. O.
1965 "Flightlessness" in the Dipper. *Condor*, 67:535–536.

Townsend, C. W.
1924 Diving of grebes and loons. *Auk*, 41:29–41.

Trautman, M. B.
1940 The birds of Buckeye Lake, Ohio. *Misc. Publ. Mus. Zool., Univ. Michigan,* No. 44.
Van Tyne, J., and A. J. Berger
1959 Fundamentals of ornithology. John Wiley and Sons, Inc., New York.
Witherby, H. F., F. C. R. Jourdain, N. F. Ticehurst, and B. W. Tucker
1940 The handbook of British birds. Vol. 4. H. F. and G. Witherby Ltd., London.

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